# THE MIOCENE TREES OF THE ROCKY MOUNTAINS

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THE living arborescent flora of the Rocky Mountain region is at the present time occupying the attention of a number of able workers, including Nelson in Wyoming, Rydberg of the New York Botanical Garden, Sudworth of the Forest Service, Ramaley, Bethel and Schneider in Colorado, Wooton in New Mexico, and others. As a result of all this activity, we are promised two manuals of Rocky Mountain botany, and a third of trees alone, so we shall have three separate and independent treatments of our woody flora to compare and choose from.

Unfortunately, those who have been so active and exhaustive in their investigations of the living flora have not cared, as a rule, to consider the historical or paleobotanical side of the subject. Many "recent" botanists seem to have a positive dislike for fossil plants, and few manifest any great eagerness to receive information about the ancestors or predecessors of the species which occupy their attention. Like all enthusiasts, the writer is filled with the idea that the matter has only to be adequately presented to command universal attention; and hence offers this discussion, not so much for the paleobotanists as for those students of living plants whose active interest may be aroused in the problems involved.

Going back from the present time, we are practically without information concerning the plants of our region until we come to the Florissant beds, assigned to the Miocene. These beds, however, contain an abundant series of remains, many of the plants beautifully preserved, as the accompanying illustrations show. They testify to a climate both warmer and damper than that of the present day, the arborescent genera including Sapindus, Ficus,[1] Diospyros, Persea, Leucæna, Anona,

[1] The determination of *Ficus* is based on the leaves. In confirmation of

etc., but so far as known no palms. Some, as *Ailanthus americana,* pertain to genera now restricted to Asia.

The determination of the age of the Florissant beds has been a matter of some difficulty, notwithstanding the large number of organisms preserved. Comparing the flora with that of the European Tertiary, I have felt satisfied that it should be referred to the Miocene, and probably to the Upper Miocene. The resemblance to the flora of Œningen in Baden, known to be upper Miocene, is most striking. Thus we have the following parallel or representative species:

| *Florissant.* | *Œningen.* |
|---|---|
| *Liquidambar convexum* Ckll. | *Liquidambar europæum* A. Br. |
| *Ulmus braunii* Heer, Lx. | *Ulmus braunii* Heer. |
| *Comptonia insignis* (Lx.) Ckll. | *Comptonia œningensis* A. Br. |
| *Porana speirii* Lx. | *Porana œningensis* A. Br. |
| *Porana tenuis* Lx. | *Porana macrantha* Heer. |
| *Acer florissanti* Kirch. | *Acer tricuspidatum* A. Br.[2] |

Many others could be cited. On the other hand, the Florissant incense cedar, *Heyderia* or *Libocedrus coloradensis* Ckll., is to be compared with *H. salicornioides,* of the Lower Miocene of Radoboj in Croatia. The Florissant redwood, *Sequoia haydeni* (Lx.), is not related to *S. sternbergi* Heer from Œningen, but to *S. langsdorfii* (Brgt.) Heer of the Swiss Lower Miocene; this species, however, survived into the Upper Miocene in Italy and Galicia. This *S. langsdorfii* has been recognized in America also from the Upper Cretaceous to the Miocene, and some of the Florissant specimens have been referred to it; but the identity of the plants from so many diverse localities and horizons is questionable, and from Florissant I think we have only one species, *S. haydeni.*

The Sequoia and Libocedrus of Florissant are both very closely related to their living Californian allies; so

it comes a discovery by Mr. Brues, who in working over the parasitic Hymenoptera from Florissant has come upon what appears to be a genuine fig-insect, apparently of the South American genus *Tetrapus* Mayr.

[2] *Acer trilobatum* (Sternb., 1825) A. Br., 1845; not *A. trilobatum* Lam., 1786.

much so that one is in some difficulty to point out any tangible differences. This is equally true of a number of other cases, of which the following are illustrative:

| *Florissant.* | *Living.* |
|---|---|
| *Pinus wheeleri* Ckll. | *Pinus flexilis* James. |
| *Pinus sturgisi* Ckll. | *Pinus tæda* L. |
| *Ailanthus americana* Ckll. | *Ailanthus glandulosa* L. |
| *Sambucus newtoni* Ckll. | *Sambucus arborescens* Nutt. |
| *Anona spoliata* Ckll. | *Anona glabra* L. |
| *Robinia brittoni* Ckll. | *Robinia pseudacacia* L. |
| *Populus lesquereuxi* Ckll. | *Populus angustifolia* James. |
| *Quercus lyratiformis* Ckll. | *Quercus lyrata* Walt. |
| *Sapindus coloradensis* Ckll. | *Sapindus drummondi* H. & A. |

So numerous are the resemblances to the living flora that one might well feel persuaded to refer the beds to the Pliocene—certainly better there than to the Oligocene or Eocene! However, the Florissant fishes, with the exception of Amia, are of extinct genera, and no less than 178 genera of insects are supposed to be extinct. For a variety of reasons, based chiefly upon a study of the insects, I believe that the Florissant period corresponds with Osborn's "Fifth Faunal Phase" (Bull. 361, U. S. Geol. Survey), in which a new fauna was invading the country from Eurasia, while connection with South America had not yet been established. Some of the Florissant groups of insects, such as the Aphididæ and Bombyliidæ, seem to represent the original American fauna uncontaminated; while others show old world types, the most significant and interesting of which is the tsetse fly (*Glossina*).[3] Osborn's "Fifth Phase" includes the Middle and Upper Miocene, and so far as may be judged, Florissant should belong near the middle of it.

The attempt to correlate the Florissant beds with other American floras ascribed to the Miocene brought out a number of difficulties. With the exception of the little-

[3] A second species of tsetse fly, *Glossina osborni* Ckll., has been recently discovered. It is only 10½ mm. long, the wing 7 mm.; the venation is normal for the genus, but the first basal cell bulges less subapically than in Scudder's species.

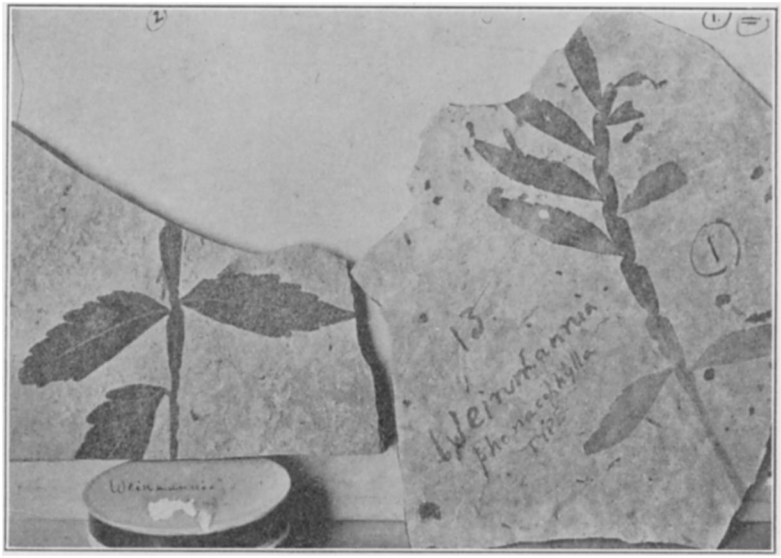

FIG. 2. *Weinmannia lesquereuxi* Ckll. FIG. 1. *Weinmannia phenacophylla* Ckll.

known formation at Elko Station, Nevada, I do not find anything which really seems to correspond with Florissant. According to the theory outlined above the Mascall beds of Oregon, which possess a varied flora, should be either contemporaneous or (more probably) somewhat earlier. Fortunately, fourteen species of mammals have been obtained from the Mascall, and these place it rather definitely in the Middle Miocene. Considering, therefore, a probable moderate difference in time, combined with noteworthy geographical and altitudinal differences, we ought to find the Mascall flora similar to, but by no means identical with, that of Florissant; and this is exactly what comparisons show.

Thus of the 77 Mascall plants (nearly all trees) referred to definite genera, no less than 56 are congeneric with those of Florissant. Of those not congeneric, five are so dubious that they have not been specifically determined. The Mascall genera not yet found at Florissant are the following:

1. *Equisetum.*—This has no significance, as it abounds in Colorado to-day, and must have been present during the Florissant period.

2. *Ginkgo.*—Represented in the Mascall by a fragment not specifically determined. This genus is not known in the Rocky Mountains later than the Laramie and Livingston, on the border line between the Cretaceous and Tertiary. As is well known, there is a single living (Asiatic) species.

3. *Thuites.*—A fragment not specifically determined. It is practically identical with *T. ehrenswärdi* Heer (Miocene of Sachalin and Spitzbergen), but that plant appears to be referable to the modern genus Chamæcyparis.

4. *Glyptostrobus.*—A genus still living in China. It was supposed to occur at Florissant, but I believe the material so referred all belongs to Sequoia. The Mascall material is not above suspicion of also being Sequoia; indeed Lesquereux so referred one of the specimens.

5. *Taxodium.*—The Mascall specimens are referred by Knowlton to the widely distributed *T. distichum miocenum* Heer, which should be called *Taxodium distichum dubium* = *Taxodium dubium* (Sternb.) Heer, originally described from Bilin. This differs from Sequoia by the deciduous leaves, which are not decurrent at the base as in Glyptostrobus. The genus still lives in our southern states.

6. *Artocarpus.*—Represented by very fragmentary material, doubtfully referred to *A. californica* Kn.

7. *Magnolia.*—Major Bendire collected a plant which Knowlton says "may well be" *M. inglefieldi* Heer. It has not been obtained by recent collectors. *Magnolia dayana* Ckll. ined. (*M. lanceolata* Lx. 1878, not Link. 1831) is listed by Knowlton as from the Mascall, but in his detailed account he says it is from Cherry Creek, which should be Lower Eocene.

8. *Laurus.*—Florissant has a species of Persea; Laurus and Persea are allied, and not distinctly separated by paleobotanists.

9. *Platanus.*—The Mascall specimens appear to belong

FIG. 3. *Sequoia haydeni* (Lesquereux). Redwood.

to three species, but none are sufficiently well preserved for positive specific identification.

10. *Prunus.*—The two Mascall species described by Knowlton are only doubtfully referred to this genus, which is of course abundant in the modern flora.

11. *Rulac.*—Generic reference rather uncertain; the genus is scarcely separable from Acer, which occurs at Florissant.

12. *Æsculus.*—This well-known living genus is repre-

sented in the Mascall by leaflets which closely resemble an undescribed Florissant species which may be a Berberis, but is certainly not an Æsculus.

13. *Grewia.*—The Mascall plant is referred by Knowlton to *G. crenata* (Unger) Heer, which occurs in Europe at Œningen.[4]

Three other genera, Phragmites, Cyperacites and Smilax, are non-arborescent, and have no particular significance.

Thus it would appear that in the Middle Miocene period Ginkgo and Glyptostrobus—if we may accept the determinations—had not yet retreated from the American continent, but survived at least in the northwest. For the rest, the Mascall flora is no doubt a lowland one as compared with that of Florissant, and this alone would explain many of the differences; thus, no one would expect to find Taxodium growing around a mountain lake.

Dr. Knowlton has described (Monog. U. S. Geol. Survey, Vol. 32, part 2) an extensive flora from the Yellowstone, which he regards as Miocene. The fossil plants of the Yellowstone National Park are divided by him into three series: (1) Fort Union, which is Basal Eocene, (2) Intermediate, said to be Miocene, and (3) Lamar Flora, also Miocene. With the first we are not now concerned, but the others must be compared with the flora of Florissant. Considering the relative proximity of the Yellowstone beds to those of Colorado, one would expect to find much similarity and even identity in the plants; but this is not the case. The difference of locality, with a moderate difference in time, might perhaps account for the diversity of species; but the Yellowstone flora as a whole does not impress one as being so modern as that of the Mascall beds or Florissant, while there is a significant *identity of species* with those of the Eocene.

I have extracted from Knowlton's tables a list of all the Yellowstone "Miocene" plants said to occur elsewhere or in the Eocene, with the following result:

[4] The African *Grewia crenata* Hochst., 1868 (not Unger, 1850), takes the name *G. populifolia* Vahl, 1790.

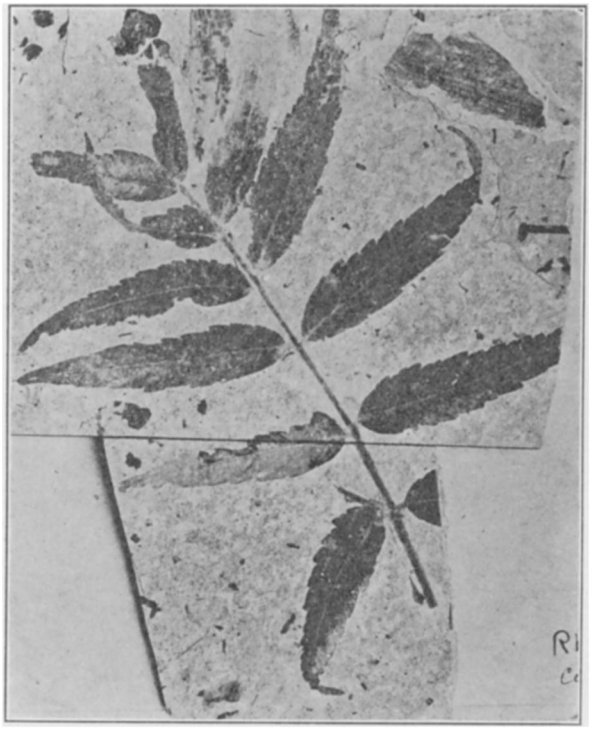

FIG. 4. *Rhus coriarioides* Lesquereux. Sumach.

1. Common to Fort Union (Eocene), Intermediate and Lamar.

*Sequoia langsdorfii* (Brgt.). Said to go down to the Laramie (Cretaceous).

*Juglans rugosa* Lx. Goes down to the Laramie.

*Castanea pulchella* Kn.

*Ficus densifolia* Kn.

*Laurus californica* Lx. Also auriferous gravels of California.

*Laurus grandis* Lx. (not Wallich). Also auriferous gravels of California.

*Platanus guillelmæ* Göpp. Perhaps also Laramie.

*Aralia notata* Lx. Also Denver beds.

* *Elæodendron polymorphum* Ward.

2. Common to Fort Union and Intermediate.

*Equisetum canaliculatum* Kn. Perhaps also in the Lamar.

*Magnolia* (?) *pollardi* Kn.
* *Ulmus minima* Ward?
*Sapindus affinis* Newby.

3. Common to Fort Union and Lamar.
*Asplenium iddingsi* Kn.
*Lygodium kaulfussi* Heer.
*Equisetum deciduum* Kn.
*Juglans crescentia* Kn.
*Ficus asiminæfolia* Lx. Also auriferous gravels of California.
*Laurus primigenia* Unger?
*Malapœnna lamarensis* Kn.
*Sapindus grandifoliolus* Ward.
*Sapindus wardii* Kn.
* *Hicoria antiqua* (Newb.).
**Ulmus pseudofulva* Lx.?

Those marked with an asterisk occur in the Fort Union only outside of the Yellowstone.

4. Common to the Intermediate and the Denver beds (Basal Eocene).
*Osmunda affinis* Lx.

5. Common to the Lamar, Basal Eocene and Laramie.
*Rhamnus rectinervis* Heer, Lx. Heer describes this from Monod, in the Lower Miocene; we may venture to doubt the identity of the American plant.

Thus we have twenty-six plants *specifically* identical with those of the Basal Eocene.[5]

6. Common to Lamar and "Green River" of Knowlton. (See also under 7.)
*Salix elongata* O. Web. Said to occur at Elko Station, Nevada, but represented only by uncharacteristic fragments. The determination of

[5] The Mascall is supposed to have five species common to the Fort Union; but of these two are doubtful, two others are the conifers *Sequoia langsdorfii* and *Taxodium*, while the fifth is *Sapindus obtusifolius*, to which a single specimen from the Mascall "seems to belong." *S. obtusifolius* was originally described from beds supposed to belong to the Washakie (Later Eocene).

FIG. 5. *Ulmus hilliæ* Lesquereux. Elm.

the Lamar plant is considered doubtful by Knowlton.

*Fagus* (*Fagopsis*) *longifolia* (LX.). Elko Station, Nevada; Florissant (very abundant) and Eocene (?) of British Columbia. The British Columbia locality is on the Similkameen River, whence come various fossil insects. Dr. Dawson (quoted by Scudder) considered these deposits Miocene. The Yellowstone collection includes about forty specimens which Knowlton

refers here, all from Fossil Forest Ridge. This is, undoubtedly, a distinctively Miocene plant, and must be accepted as pertinent evidence. The determination must be presumed to be correct, though it may be pointed out that various other leaves have almost exactly the same venation and appearance. This is especially true of the species of Zelkova, to which genus Engler (1894) actually referred *F. longifolia,* though the discovery of the fruit has since shown that it is not related thereto. *Ulmus plurinervia,* as figured by Heer from Alaska, is also almost exactly like *F. longifolia;* it is considered doubtfully Eocene, but Knowlton has recognized it in the Mascall (Miocene). From the shape of the base, and other features, it seems to me certain that the Alaskan plant is not the original *U. plurinervia,* of which Unger gives four figures in the Chloris Protogæa. The latter is decidedly more elm-like in appearance.

*Corylus macquarrii* (Forbes) Heer. This plant, as recognized in America, is a Fort Union and possibly Laramie species; recorded also from the Eocene (?) of Alaska.

*Diospyros brachysepala* A. Br. As recognized in this country, this is a Laramie and Fort Union species; the record from Florissant I believe to be erroneous.

None of the above belong to the genuine Green River series; three are quite without significance as indicating Miocene affinities, but the *Fagus* stands out as a solitary Miocene representative.

7. Common to the Lamar and the Auriferous gravels of California. (See also under 1 and 3.)

*Juglans leonis* Ckll. Two specimens in the Lamar.

*Populus balsamoides* Göpp. Also Miocene (?) of Alaska. Known in the Yellowstone only from a fragment, which certainly can not be positively determined as *balsamoides:* in fact, it shows

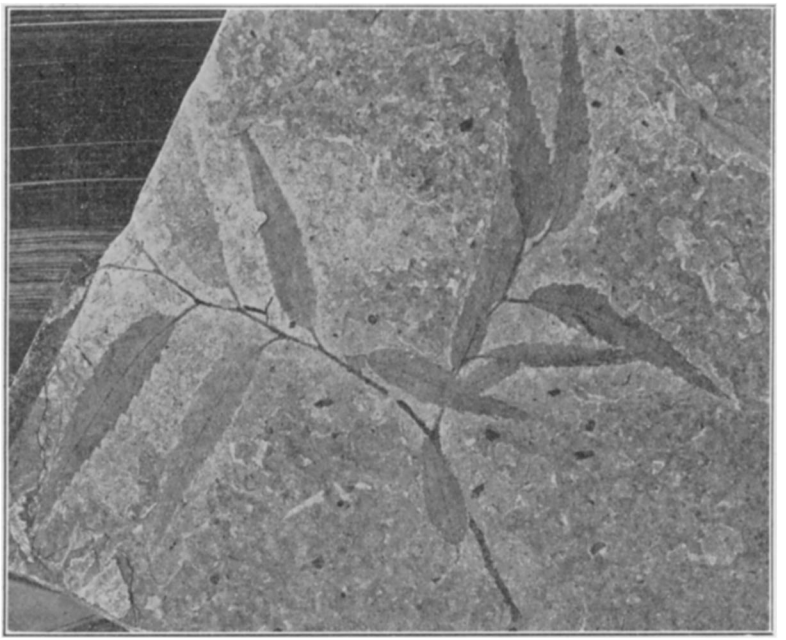

FIG. 6. *Myrica drymeja* (Lesquereux).

some differences, at least as compared with the original European *balsamoides*, which ought to be specific.

*Salix varians* Göpp. Eocene (?) of Alaska. The Lamar plant is a fragment, and according to the figure, the margin is quite unlike that of the European *varians*.

*Salix angusta* A. B. Said to occur also in the Basal Eocene and true Green River. The Lamar material consists of doubtful fragments.

*Quercus furcinervis americana* Kn.

*Ficus shastensis* Lx.?

*Ficus sordida* Lx. A mere fragment from the Lamar.

*Ficus asiminæfolia* Lx. Very indifferent material from the Lamar. Also Fort Union.

*Magnolia californica* Lx.? The Lamar plant is represented by a single specimen, "so much

broken that its positive identification is not possible" (Knowlton).

*Persea pseudocarolinensis* Lx. The Lamar specimen figured, "the best one found," consists of the upper half of a leaf; what there is of it appears to agree with the Californian species, although it has more lateral viens.

*Rhus mixta* Lx.?

*Aralia whitneyi* Lx. Also in the Intermediate. None of the Yellowstone specimens are perfect, but they appear to belong to this handsome species.

Thus the species common to the Lamar and Auriferous gravels, *but not known from Basal Eocene*, are few, and in several cases of doubtful identity. As the reference of the Lamar to the Miocene rests wholly on the resemblance of the flora to that of the Auriferous gravels, with the exception of the indication afforded by *Fagus longifolia,* it must be considered at least somewhat dubious. It is also to be remarked that eleven species of plants are supposed to be common to the Yellowstone Fort Union and the Auriferous gravels, although two of these, at least, are doubtfully from the gravels, while in four or five cases the Yellowstone material is fragmentary or doubtful.

It is one thing, however, to recognize distinct elements in common between the Auriferous gravels and the Lamar, and another to prove the latter Miocene thereby. The former may be conceded, the latter I think not.

Lesquereux enumerates thirteen species from the Auriferous gravels which are almost identical with living species; he also cites seventeen which are evidently, but not very closely, related to living ones. Of the thirteen, four are enumerated from the Lamar; of the seventeen, not one. Of the four common to the Lamar, three are dubious, and only *Juglans leonis* (a species represented to-day by the Asiatic *J. regia*) appears to be of satisfactory standing.

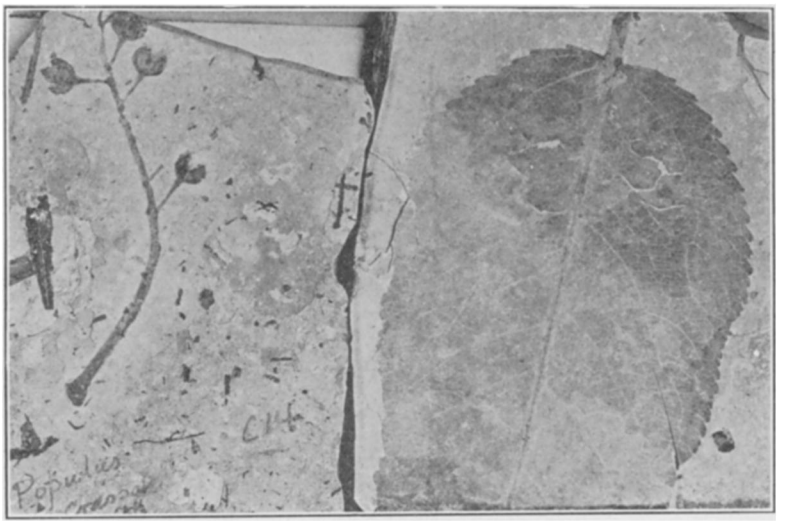

FIG. 7. *Populus crassa* (Lesquereux). Cottonwood; probably fruit of *P. lesquereuxi.*
FIG. 8. *Populus lesquereuxi* Ckll. Cottonwood.

Four species of the Auriferous gravels are said by Lesquereux to be identical with Miocene plants, but are all unsatisfactory, as follows: (1) *Fagus antipofii;* perhaps goes to the Laramie, and the Californian specimen was only half a leaf. (2) *Populus zaddachi;* supposed to go down to the Basal Eocene. (3) *Ficus tiliæfolia;*[6]

FIG. 9. *Salix ramaleyi* Ckll. Willow.

[6] *Ficus tiliæfolia* (A. Br.) Heer, 1856, has priority over *F. tiliæfolia* Baker, Jn. Linn. Soc. **21**: 443 (1885), from Madagascar. The latter may become *Ficus bakeriana* n. n.

said to go down to the Laramie. (4) *Aralia zaddachi;* of uncertain determination, one of the specimens was *Platanus dissecta.* None of these is found in the Lamar, but *F. antipofii* is in the Yellowstone Fort Union.

Eight other species from the Auriferous gravels are stated to be allied to Miocene species, five of these being also related to living plants. One of the five, *Juglans oregoniana,* has since proved to be from the Mascall, and not to occur in the Auriferous gravels. The other three are as follows:

*Ficus sordida* Lx. Allied to, or perhaps identical with, *F. grœnlandica* of Greenland. A fragment referred to this has been found in the Lamar.

*Ficus mensæ* n. n. (*F. microphylla* Lx., 1878, not Salzm., Mart. Fl. Braz. 4: 93). Allied to *F. planicostata*—but this is a species of the Basal Eocene and Laramie.

*Aralia whitneyi* Lx., said to be allied to an Evanston species, which would be Eocene.

It is thus apparent that the Auriferous gravels flora has no decisive Miocene affinities, but is composed of two sets of plants, one related to living forms, the other to those of the Eocene. It is known to be a mixed lot, and when I recently suggested to Dr. J. C. Merriam, of the University of California, that it might perhaps be partly Pliocene and partly Eocene, he replied that this might indeed be the case.

It is further to be remarked that Knowlton formerly regarded the Mascall flora as having affinity with that of the Auriferous gravels; but he subsequently discovered that certain of the species he had most relied on were really confined to the Mascall, and did not occur in the gravels at all. "This correlation therefore fails," he states, and the absence of relationship stands as an argument against the Miocene age of the gravels.

The conclusion seems to be legitimate that the Yellowstone Intermediate and Lamar floræ are Upper Eocene, or at least older than Miocene. Were they really Mio-

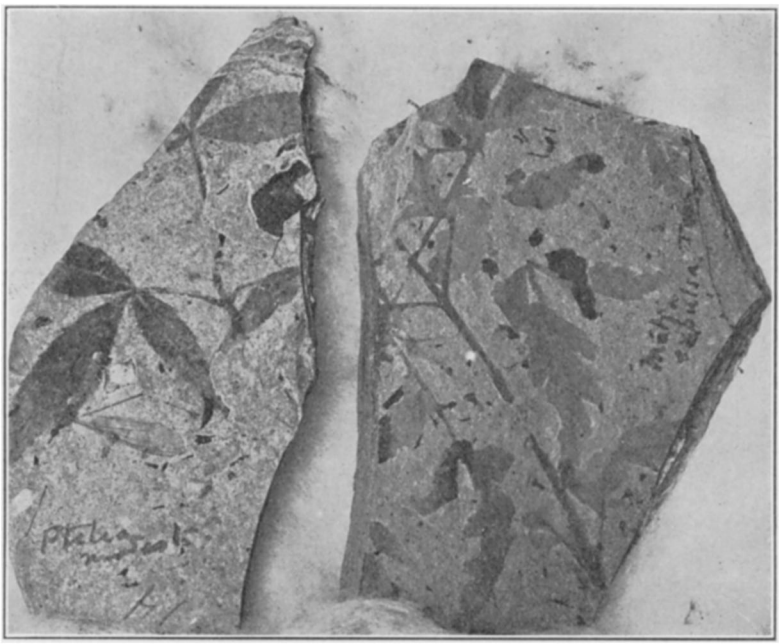

FIG. 10. *Ptelea modesta* (Lesquereux). FIG. 11. *Melia expulsa* Ckll.

cene, with so much resemblance to even the Basal Eocene, the Florissant flora, to get as far on the other side as its lack of affinity would suggest, would have to be projected somewhere into the future! If this opinion is in any degree correct, Florissant remains as the only Rocky Mountain locality for Miocene plants, so far as known.

The accompanying figures, all taken from specimens obtained at Florissant by the University of Colorado expeditions, will give a good idea of the material from that locality. Nowhere else in America are Tertiary plants so well preserved. As compared with the Eocene flora, and especially the Basal Eocene, the Florissant trees are more diverse in type, with usually smaller leaves, which are often compound. Excessively moist conditions are not indicated, though there was evidently much more moisture than at the present day. Some of the plants are even somewhat xerophytic, indicating that the higher slopes may have been relatively dry. Osborn remarks on the evidence of increasing summer droughts

in the Middle Miocene. So far as the mammals are concerned, this is chiefly indicated by the plains fauna. Owing to the generally higher temperature, the air was probably moister than at present, but the moisture may have carried farther, to be precipitated on the mountains. Thus the conditions on the plains and towards the sea may have resembled those of Southern and Lower California to-day, with a comparatively damp atmosphere but little or no preciptation during a considerable part of the year. The desert fauna and flora of the southwest is a highly specialized one, which has certainly not come into existence since the Miocene, at least as regards its fundamental types; so it becomes necessary to postulate a desert region during Miocene times, and no doubt much earlier. Whether we shall ever know much about the Tertiary deserts from fossil remains is perhaps questionable, though we certainly have evidence of a semi-desert fauna, as is illustrated by the large tortoises of the Upper Miocene. The Florissant beds afford us a wonderful insight into the mountain life of the Miocene, and must have a continually increasing significance in relation to the evolution of the fauna and flora of this continent. Most unfortunately, they have as yet yielded no recognizable mammalian remains, but I am convinced that these will eventually be found. The beds are far from being exhausted, and comparatively little digging has been done at the place where fragments of a mammal were obtained—a locality which I shall be glad to describe in detail to any one who cares to go and try his luck. In the meanwhile, large collections both of plants and of insects, already obtained, remain to be investigated and reported upon, but for various reasons the work proceeds slowly.